Early Journal Content on JSTOR, Free to Anyone in the World

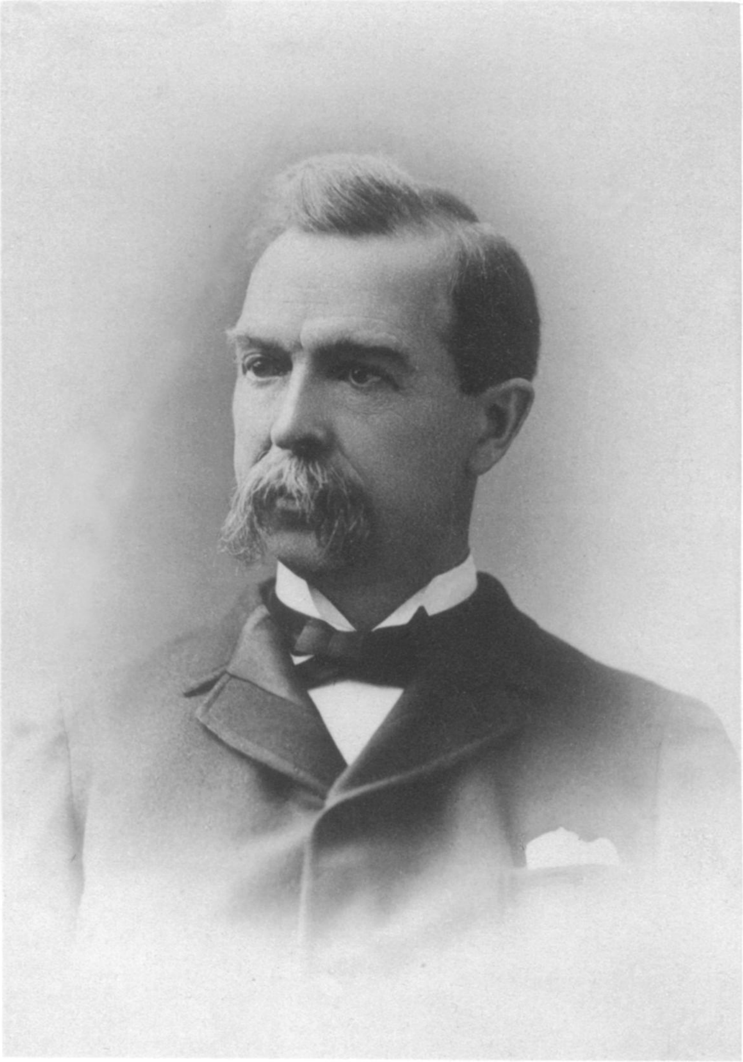
This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.



T. F. Allen

VOL. 30 NO. 1

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1903

# Problems in the Study of Plant Rusts*

BY J. C. ARTHUR

The inception of the Botanical Society of America was the crystallization of a desire on the part of a number of zealous botanists to encourage research and to promote the general welfare of the science in America by concerted action. The result has been conspicuously successful. Beside providing an atmosphere of tolerance, expectancy and discriminating appreciation for the presentation of papers, by no means a small honorarium in the intellectual remuneration of the earnest investigator, a fund of money has been provided in accordance with the original intent of the founders, with which to assist and encourage research. The first distribution from this fund is made at the present meeting. It is a matter of congratulation that the wisdom shown in devising the plan for its creation and the business sagacity brought to bear in its management have enabled the society to offer a sum not only large in consideration of the age and membership of the organization, but equally noteworthy in comparison with any similar fund provided by American societies of whatever age and size. Without question the society is established squarely upon the doctrine of research, and the other benefits emanating from a body of this kind, which are by no means few, inconspicuous, or undeserving of consideration, are as the glory of a noble tree with its foliage, flowers and fruit, useful and luxuriant in proportion to the quantity and quality of its nutriment.

---

*Delivered at Washington, D. C., December 31, 1902, as an address by the Past President of the Botanical Society of America.

[Hereafter the exact date of publication of each issue of the BULLETIN will appear in the succeeding number.]

In the selection of a subject for the present address it has seemed fitting that the central thought of the society should find a measure of expression, and therefore I have brought together some of the suggestions, entanglements and problems that have arisen during a series of investigations into the life histories of a number of the plant rusts. I do this with the more alacrity as it enables me to bring before you, and possibly to introduce to some of you for the first time, a remarkable class of plants of great scientific and economic importance.

The plant rusts, or Uredineae, are microscopic fungi, strictly parasitic in their nature, inhabiting all classes of flowering plants and ferns. The mycelial body of the fungus consists of colorless hyphae which ramify through the tissues of a larger or smaller part of the host. Sometimes they permeate every part of the plant above ground, but more usually are confined to certain areas, often very small and circumscribed. It is at all times difficult to distinguish this vegetative part of the fungus from the cellular structure of the host, unless special differentiating methods are employed.

On the other hand the reproductive parts are comparatively prominent, being yellow, red, brown, black or some characteristic tint, and with few exceptions are formed at or near the surface of the host, and of sufficient size to permit recognition under a hand lens or often by the unaided eye. These fruiting bodies are generally dehiscent, exposing the spores as a waxy or powdery layer. When produced abundantly, and of an orange or brownish color, the supporting plants have the appearance of being dusted with iron rust, which has suggested the now common name of plant rusts. The most generally recognized examples are the rusts of wheat, oats and other grains, which cause a loss to the people of this country of many millions of dollars annually, often equalling that caused by the Hessian fly, chinch bug and all other insect and fungous enemies combined.

The fruiting parts and especially the spores are the only portion of the rust fungus seen or recognized by the general observer, the botanical collector, or the average student. Not only are the spores readily seen, but as a rule they are easily removed and examined under the microscope, needing no preparation except moistening with a drop of water. Moreover, dried specimens keep indefinitely in all their perfection of form and intimate structure, and also as a rule of color. Hence it has come about that the description of species and the general classification has been founded almost exclusively upon the spore forms. This was a necessity at first; but it is a crude and artificial method. It has led to no clearer understanding of the real relationships of the species than did the Linnaean system for flowering plants, with its countings of stamens and pistils. Yet this comparison does scant justice to the intricacies of the subject, and the difficulties under which the systematic uredinologist has labored.

The student of phanerogamic plants, even back to the days of Linnaeus, has been well aware that few of the plants which come under his observation have more than one kind of flowers. The flower contains the pistils and stamens, from the interaction of which arises the fruit. Sometimes, to be sure, the pistils and stamens are in separate flowers on different parts of the plant, or even on different plants, as in the willows and poplars. But with rare exceptions, so rare as to have no appreciable effect upon the development of the subject, no material difficulty has been experienced in detecting the essential organs of reproduction, and no question has arisen regarding their association with the fruit which follows their appearance.

In order to come to an appreciation of the conditions existing among the rusts, and some of the difficulties besetting systematists in trying to unravel relationships, let us suppose some changes in the phanerogamic world. Let us begin by supposing flowers to be wholly suppressed, so completely in fact that the fruit would appear to arise from swollen buds, as figs do in fact, only in the case we are supposing the flowers are so totally suppressed that even the microscope reveals no trace of them. Now in this imaginary world each kind of tree, shrub and herb may bear not only one form of fruit, but two, three, four or even five forms as different as peaches, acorns, chestnuts, beans and currants. Two or more of these may occur at the same time in any variety of combination. Often delicate, peach-like fruits will be produced in a succession of crops throughout the summer, then in the fall a crop of acorn-like fruits that are not injured by hanging on the plants all winter. But more curious than this, the seeds from one kind of fruit rarely produce a plant that will bear the same kind of fruit again. If the acorn-like seeds are planted, the plants that are grown may bear acorns, but are rather more likely to bear fruits enclosed in sacs like chestnuts. To some extent this alternation of forms appears to be haphazard, at least dependent upon conditions not understood, but to a large extent it seems to be a question of the species. If acorn-like fruits from one species of plant are sown they give rise to plants bearing currants, soon followed on the same plants by chestnuts. When the chestnuts from this species are sown the resulting plants bear peaches, followed on the same individual plants by acorns. But there is no predicting what combinations will occur in any one species. When different kinds of fruits are found on the same individual they are known, of course, to belong to the same species, but when on separate plants their connection can only be told by actual planting. To further complicate matters one kind of fruit, the currant we will suppose, has seeds that cannot be made to develop into a plant, although they will germinate; and their purpose in the economy of the plant cannot be conjectured.

Let us fancy now that all plants of this imaginary world are exceedingly small, even the largest trees not being half the size of a pin, while the smaller plants are mere specks, in fact microscopic. How long do you think it would take botanists, with a flora of this sort, to become acquainted with the different varieties of each kind of fruit, and to connect the several forms into the cycle of true species?

In this fanciful sketch I have tried to portray some of the simplest conditions that exist among the rusts, using the fruits of currants, chestnuts, peaches, acorns and beans to represent respectively spermogonia, aecidia, uredo, teleutospores, and amphispores, in order to show how complicated they are in comparison to the conditions that exist among flowering plants. If I have succeeded in making my analogy clear, it can be readily understood that the earlier botanists gave names to each spore-form, believing it to represent the whole species. Thus *Uredo segetum* was the name of the red rust of wheat, *Puccinia graminis* the black rust of wheat, *Aecidium Berberidis* the cluster-cup rust of barberry bushes; and they certainly appear distinct enough to belong to different genera, although now we know them to be forms of one species. The ablest writers, down to the days of DeBary at the middle of the nineteenth century, described all species of Uredineae under the form-genera, each species thus being divided among as many genera as it had kinds of spores. Even to the present time the practice continues as a matter of convenience. Yet as early as 1810 Friedrich von Strauss entered a protest against placing such obviously connected forms as the *Uredo* and *Puccinia* of wheat under two genera, but in his attempt to readjust the forms under a suitable nomenclature he illustrated what deplorable systematic work can be done with a good logical basis but a lack of accurate observation. While he believed that many *Uredo* and *Pucciniae* were genetically connected, he made a vigorous objection against the association of certain *Aecidia* with these forms. In a communication to the Wetterau Society he says: "The assumption that these fungi [*i. e., Uredo* and *Puccinia*], at least *Uredo segetum*, originate from the scattered red dust of *Aecidium Berberidis*, nature had already refuted before experience. Numerous examples are known to me, where the digging out of barberry hedges did no more good than did previously the destruction of crows in the American colonies." I do not know what action was taken in these early times against crows in our country, but I know that the colony of Massachusetts in the reign of George II. passed a law entitled "An Act to prevent Damage to English Grain arising from Barberry Bushes," with very stringent provisions for its enforcement, which law remained on the statute books twenty-five years.

Von Strauss was certainly in error in his conclusion that digging out barberry bushes did no good, as he might have learned, had he examined Marshall's "Rural Economy of Norfolk," a most readable book that had at the time passed through more than one edition; and, moreover, he was fundamentally wrong in assuming that there could be no causal connection between such apparently diverse fungi as the cluster-cups of the barberry and the yellow rust of the wheat, as was proven by DeBary experimentally a half-century later.

It is to DeBary that we are indebted for the first clear insight into the life-cycle of the rusts. He brought to their study more rigid methods of observation than his predecessors, and above all he first used culture methods, which have since become the crucial test of all uredineous species, and the key to the complex cycle of their development. It was in January, 1865, that Professor Anton DeBary, of Freiburg, laid before the Berlin Academy a paper dealing especially with the development of *Puccinia graminis* and its connection with *Aecidium Berberidis*. It was the opening of a new era in the study of plant rusts. Botanists had already become somewhat familiar with the succession of aecidial, uredo and teleutosporic forms among the rusts, but DeBary took up the most difficult, complex, and enigmatical of all the rust species, which at the present day even is very far from being fully understood; I refer to the black rust of grains, especially of wheat, which economically as well as scientifically is no mean problem, as it causes a loss in this country alone of some millions of dollars a year. He studied the germination of the spores from the wheat plant, and acting upon a suggestion derived from the practical farmer sowed the teleutospores upon barberry leaves, and raised cluster-cups. For more than a century the close observer of farm crops had strenuously maintained that barberry bushes near wheat fields increased the amount of grain rust, and the botanist had scornfully laughed and asserted that no known fact in nature warranted such an absurd idea; but DeBary vindicated the farmer.

The following year DeBary announced that oat rust bears its aecidia upon buckthorn leaves, and that rye rust has its aecidia upon alkanet, an Old World weed. The same year Oersted, a Danish botanist, published the results obtained by the DeBary culture method, showing that the rust of cedar trees is connected with the cluster-cups on leaves of pear trees.

Thus was the new doctrine of heteroecism established: the existence at different periods of growth of unlike forms upon totally unlike host plants. Its acceptance, however, was slow, and the culturists were few. During the seventies and eighties the attitude of most botanists was far from cordial. A few accepted the doctrine, but it exerted little influence upon the course of development of the general subject of uredinology.

It was, however, during this period that cultures were made by

Farlow, Thaxter and Halsted upon the connection between cedar rusts and the aecidia on Pomaceae, from which most of the present knowledge of American *Gymnosporangia* has been derived, a genus of rusts especially North American in the number and diversity of its species. And it was during this period that Plowright in England cultivated the rusts and ably presented the claims of heteroecism. In Germany Rostrup, Schröter, and Winter made cultures, and the last two, more than all others of this period, permitted the doctrine to influence their systematic treatment of the order. Each began, and carried well forward, the fungous flora of a large region: the Kryptogamen Flora von Schlesien and the Kryptogamen Flora von Deutschland, Oesterreich und der Schweiz, in which the Uredineae were elaborated in a manner yet unapproached. These two works, with Burrill's Parasitic Fungi of Illinois, Part I., which was issued during the same period, and inspired by Winter's work, are the only systematic handbooks of the order, founded upon a critical study of specimens, that are available to the American collector even to this day, although they were published from fifteen to twenty years ago. Since that time the number of known species has more than doubled, and the volume of information about them has quadrupled.

We may pause a moment here to recall what Sachs, writing near the beginning of the era of culture studies, said in his History of Botany about parasitic fungi, of which the Uredineae are the chief representatives. He characterized them as "the most attractive objects in the whole field of mycology," and said that "here were difficulties in abundance, here were the darkest enigmas with which botany has ever had to deal." Among the difficulties he had in mind were "to discover what properly belonged to one cycle of development" and to find where in this cyle the sexual fusion occurs.

Regarding sexuality of the rusts there is still dense ignorance, but regarding the exact cycle of development great advances have been made. DeBary supplied the key to this garden of knowledge, and during two or three decades some twenty botanists essayed the tedious but interesting task of growing one or more species of Uredineae and tracing the succession of forms through a life-cycle, some sixty or seventy heteroecious species being thus investigated. During the last decade of this era, however, more botanists have worked at solving these riddles, and some of them have made the work continuous from season to season, taking great pains to explore suggestive by-paths. The results have not been confined to a knowledge of life-cycles of individual species, but have brought to view some unexpected facts of far-reaching significance, regarding the limits of species and their biological behavior. Doubtless many who listen to me to-day also heard the vice-presidential address of Professor Farlow before the botanical section of the American Association for the Advancement of Science in 1898, in which he traced with great clearness and with many side-lights, the modification and broadening of our conception of species through recent cultural work on rusts. It would be superfluous to retrace the ground, even were I capable of equalling the admirable presentation, but some phases of the subject, which have since become prominent, may well be mentioned here.

One of the most eminent investigators in this line of research, to whom science and also the world at large owes much for his work on grain rusts, is Dr. Eriksson, of Stockholm. The great unfolding and clarification of a subject of such vast economic importance justly merited the gold medal and other honors, which have been bestowed. That what had previously been rated three species of rusts, *Puccinia graminis*, *P. rubigo-vera* and *P. coronata*, have been found under the search-light to be seven or eight species or possibly ten or twelve, with numerous specialized forms or so-called biological species, is some indication of the thoroughness and extent of the labor. Practically it has been of the greatest value to know that the rust of grains belonging apparently to one species cannot usually be spread by the uredospores from rye to wheat, rye to oats, oats to barley, or in general from one kind of grain to another. But mapping out the possible distribution of each species of grain rust still requires a vast amount of work, as not only the cultivated grains are involved, but many species of wild grasses.

In passing, attention may be called to a remarkable and seemingly anomalous property belonging to the principal grain rusts, that of attacking hosts standing in two or more tribes of the Gramineae. Of the hundreds of other species of rusts inhabiting grasses it is probably safe to assert that not one spreads to hosts outside of a single tribe. No full explanation of this is yet forthcoming, but when found it is likely to throw a flood of light upon the true nature of parasitism.

We return from this digression to note that Eriksson has vigorously attacked the difficult problem how the rust is carried through the winter and again becomes a menace to the farmer in northern regions, where the mycelium is not perennial and where barberry and alkanet or other suitable host plants are wanting on which the cycle of development can be completed. In trying to account for the facts he has elaborated and widely published a micoplasma theory: the symbiotic and intimate association of the protoplasm of the host and its parasite, unseparated by cell walls. This theory has not been accepted by most botanists, and since the recent publication of Marshall Ward's researches upon the rusts of the genus *Bromus*, appears to have no authentic or even probable facts upon which to rest. The studies of Carleton upon the American *Euphorbia* rust, in which it was found that the mycelial fungus may be carried over the winter in the seeds, may throw some light upon Eriksson's anomalous results, without invoking a micoplasma theory. We may, indeed, believe that to solve the practical problems of the mode of propagation and the power of infection of the several grain rusts requires all the astuteness and skillful experimentation that can be brought to bear; and the repeated failures of the ablest investigators only emphasize the difficulties.

The expansion of knowledge through DeBary cultural methods cannot be better illustrated than by citing the results attained by Dr. Klebahn of Hamburg with the willow and poplar rusts. This investigator stands foremost among those who have used each season's work as a basis for shaping the work of the following season, and who *pari passu* with cultural results have studied morphological characteristics, combining the two classes of data into taxonomic expression. Most systematists have contented themselves with listing the willow rusts under *Melampsora salicina* and the poplar rusts under *Melampsora populina*, or equivalent names. This was the disposition of them made by Winter and Burrill. Some have essayed segregation, but with an unsteady hand. Thümen in 1879 described seven species of willow rusts and

Schröter in 1887 recognized four willow rusts and three poplar rusts. The characters for these were drawn chiefly from the uredospores, although the latter author was guided somewhat by the limited cultures of Rostrup and Nielsen.

The matter presents a wholly different aspect when we turn to the conclusions reached by Klebahn. From an external knowledge of the species we are presented with an intimate knowledge, and from conjecture we pass to reasonable certainty. It is somewhat startling, nevertheless, to find that the original single willow rust has become fourteen, and the one poplar rust has become seven. One of the willow rusts, quite unsuspectedly, proves to be autoecious, having its aecidium on willow leaves along with the uredo and teleutostage; all the other species are heteroecious, with their aecidia on *Larix*, *Euonymus*, *Ribes*, *Orchis*, *Allium* and *Galanthus*. The poplar rusts are all heteroecious, with their aecidia on *Larix*, *Pinus*, *Allium*, *Mercurialis*, *Chelidonium* and *Corydalis*. Most of these species can be told from one another by morphological characters quite as readily and as certainly as can the species of *Viola*, *Crataegus* and *Antennaria* in the present congested condition of these genera; but some of them are difficult to distinguish in this way. For instance, the five species which occur on *Populus tremula* can scarcely be told apart unless the aecidial host is known.

As an incidental piece of information it may be stated in this connection that all the willow and poplar rusts investigated by Klebahn are European. Although similar rusts are common in this country, and often sufficiently abundant to be destructive to their hosts, yet none of them has so far been identified with European species; and, moreover, the most common forms may be assumed, with some degree of certainty, to be distinctly American.

But to return to the question regarding species that are morphologically similar, but ecologically dissimilar; it appears to be possible for all five of these *Melampsorae* on *Populus tremula* to grow side by side on the same individual leaf, in which case the uredospores would be practically indistinguishable by any direct morphological or cultural test, the teleutospores could only be told apart by ascertaining what species of host they could be made to infect, while the aecidia would be known by the particular host they inhabited. The aecidial hosts in this case are exceedingly diverse and represent about the whole gamut of the spermatophytes. A similar case is that of the American *Carex* rusts, having aecidia on the three large intergrading genera *Solidago*, *Aster* and *Erigeron*. Although they have not yet been studied thoroughly enough to speak with entire confidence, still it is evident that they have very slight morphological distinctions, and possibly have no constant differential characters except the association of the aecidial host.

The practical question that arises is in regard to the systematic treatment of such forms. Shall they be classed as species, subspecies, varieties or races? This is not so much a question of fact, as of convenience and intelligent interpretation. No one, nowadays, believes that species are circumscribed in any definite manner, but that usually they exhibit developmental mobility which is recognizable in all manner of intergradations and differentiations. What is wanted of systematic botany is a nomenclature that expresses in a fair way the relation that exists between forms as found in nature. It will at the best be an imperfect and unequal interpretation of the facts, but it surely ought to be employed with understandable uniformity.

Botanists, I believe, have not often gone to the extreme of some of their co-workers in allied sciences. From a communication in a recent number of Science it appears that "in ornithology, and especially in mammalogy, perfectly good species are often so similar in size and color that even the expert can not satisfactorily identify them from descriptions. * * * They present to the eye differences that are sufficiently impressive but which, owing to the imperfection of descriptive terms, can not be adequately expressed in keys or in diagnoses." If one may venture an opinion on matters outside of his own domain, forms which differ by such intangible characters as here indicated, so that they can not be expressed on paper, are not species in the generally accepted sense. They may be deserving of names, and be of great interest to the specialist, and may serve most important ends as basis for particular inquiries, but their rank is not that of true species in the general sense; at least, I think this may be safely asserted if plants are in question.

I need not speak of the validity of physiological species as adopted by students of bacteria and yeasts; they have their place. In fact, I do not deem it necessary to bring up for discussion the hackneyed subject of what constitutes a species. Even were I polemically disposed, it would be hazardous; but I have in mind only to call attention to the hyphenated nomenclature so effectively used by Klebahn, Fischer, and others, to indicate dichotomous parasitism. For instance, what has been considered *Melampsora populina* occurring upon *Populus nigra* is found to be separable by cultures into two forms, one having its aecidium on *Larix* and the other on *Allium;* these two forms are named by Klebahn *Melampsora Larici-populina* and *M. Allii-populina*, although they may not be morphologically distinguishable.

Such names are descriptive, and a great help in following the diversified results of cultures. Whatever their status in strictly systematic work, they would appear to have their use and be permissible for cultural studies. But when the conclusions of the culturists are transferred to systematic botany the provisional nomenclature must necessarily be subjected to the rigid laws of priority; moreover, questions regarding the propriety of accepting the cultural forms as species must also be settled to accord with general usage. In making such changes it is doubtful if the systematist could safely rank as species forms that have not a reasonable morphological distinctness in addition to their host connections. The morphologically distinguishable species, like *Melampsora populina*, may be separated into varieties showing selective parasitism, like the varieties *Larici-populina* and *Allii-populina*. If some such method is not adopted, we may well be appalled at the probable condition of systematic uredinology a few years hence.

At present there are only about a dozen culturists active. In North America alone a hundred species of grass and sedge rusts are known, which of course does not include all the heteroecious forms. Of these less than twenty have been traced to an aecidium, and none have had more than a preliminary investigation. In what proportion these hundred species are likely to exhibit selective parasitism can not of course be told, but it is likely to be large. What is the future collector to do, if when he turns to his manual he finds that on the host he has in hand there are recorded from two to a dozen species, none of which can be told except by a cultural test? Would it not be better that he should find one species recorded for his host, having from two to a dozen varieties separable by cultures? Moreover, would not this accord better with usage in other fields of plant life, and at the same time give a more just conception of relationship?

Difficulties in this line are not confined to the heteroecious rusts. The autoecious species are likely to prove quite as perplexing and intricate when studied with equal thoroughness. The American species of rust on *Euphorbia*, called *Uromyces Euphorbiae*, has been somewhat examined culturally, and four cultural species have been found respectively inhabiting *Euphorbia maculata*, *E. nutans*, *E. dentata* and *E. marginata*. Both aecidiospores and uredospores have been used for the cultures, and in no case has it been possible to transfer the rust of one of these hosts to another; morphological characters by which to distinguish them, however, have not been found. Fancy the systematic situation for the *Euphorbia* rusts, when the other hosts are examined, not only of the eastern United States for which Britton's Manual gives thirty-six species, but of the western regions, and especially of Mexico and other warm countries where Euphorbias attain a greater development, many being woody and even tree-like, and where rusts on them are especially abundant.

But I ought not to weary you with more of this perplexing topic. Let the culturists and the systematists fight out their battles. It is difficult to foresee whether the outcome will be the establishment of order or the release of pandoric confusion.

Probably no part of the many-sided subject of the rusts is superior in interest to the fact of their complete parasitism. They not only vegetate inside the host without destroying it, but even at the fruiting points the tissues are rarely killed. On the contrary they often exert a stimulating effect upon the cells of the host, so that the tissues remain green, especially about aecidia, when other parts of the organ are yellow and dying. Another phase of the stimulating effect is seen in hypertrophied development. So intimate is the association of parasite and host that as a rule the vigor of the parasite is directly proportional to the vigor of the host. Every culturist soon learns, that to have success in his work he must employ strong, rapidly growing plants. Even if he succeeds in infecting weak plants, the fungus will rarely come to a satisfactory fruitage. Usually all growth of the rust stops with the death of the host, although in a few cases, especially in the genus *Melampsora* and *Coleosporium*, the teleutosporic development continues for a time after the leaves of the host have fallen to the ground, as among the willow and poplar rusts. This physiological fact supports morphological facts, which place these genera among the lowest of the Uredineae in the scale of development, and ally them to saprophytic forms. Probably the primitive Uredineae were wholly saprophytic and largely unspecialized as to host, but as they gained in power to attack living tissues, they became more and more restricted in their dietary choice. When we remember what remarkable chemotactic sensitiveness the germinating spores of many fungi possess, saprophytes as well as parasites, it is not difficult to account for a high state of specialization in the selection of a living substratum within which to function and from which to draw food-supplies.

This specialization of the parasite must have begun and been carried on in large part along with the specialization of the host, and we should be prepared to find a parallelism in their association. The large and peculiar genus *Ravenelia* is all but confined to the leguminous families of flowering plants. The genus *Phragmidium* is largely parasitic on the Rosaceae. The species of *Gymnosporangium* are found only on certain coniferous hosts, and their aecidia on the Pomaceae. And so we might continue, showing that there is some association, not at present wholly explainable, between certain tribes and genera of rusts and certain families and tribes which serve them as hosts, and in many cases this association is very closely circumscribed.

The knowledge of this parallelism is an important help in keeping us at the present time from falling into the error, so common among the older systematic students of the rusts, of assuming that forms on widely related species of hosts, however similar in appearance these forms may be, might belong to one species, without securing rigid proof. Not until recent years would it have been considered strange to announce that a certain species of rust had been found upon Borraginaceae, Asclepiadaceae and Compositae. A common expression has been that the form was found "on various species of grasses and sedges." But such instances as these are not known at the present day. There is no species known that inhabits grasses *and* sedges. Moreover, it is rare that any species of rust will be capable of growing on all the genera of a large family, or even on all the species of a large genus, unless these be remarkably homogeneous.

Is it not apparent that the exact identity of the species of host on which a rust is found constitutes information for the proper study of its systematic relationship and often of its specific identity only second to the characters drawn from the fungus itself? No rust can be considered apart from its host; the parasitism is so closely wrapped up in the evolution of the species that to ignore it would be folly. Many collections of Uredineae are rendered nearly worthless for study because the collector neglected to determine the host, or to include material in the collection by which the student could determine it. So little importance has been attached by collectors to this part of their work that rarely are characteristic parts of the host included, so that the student may independently satisfy himself of the correctness of the determination, and so that in after years the determinations may be revised, if necessary. It is usually forgotten that the classification of phanerogamic plants has not yet become perfect, and every change in their nomenclature must be reflected in the nomenclature of the uredineous hosts. Evidences of the lack of appreciation of the importance of correct determination of the hosts of the Uredineae are shown in many ways; I may cite an instance coming to hand while preparing this address. In an exhaustive treatise on the flora of the island of St. Croix about fifteen hosts are mentioned for the few rusts that had been collected, and four of these are not listed in the phanerogamic part of the work. Again in that admirable flora of Alabama, issued some time ago, the lifework of Dr. Mohr, a number of uredineous hosts are mentioned not in any way referred to under the families of phanerogams where they should appear. Another source of annoyance and of misinformation is the not infrequent failure of uredinologists to recognize hosts under their synonymic aliases. It is very easy at the present time for a plant to go masquerading under several names. Of course, the well-informed ought not to be deceived by these disguises, and if they were sufficiently on the alert they probably would not be. Yet it is not rare to have new species of rusts described because the describer did not recognize the host under its latest name, as an old-time acquaintance. This failure of recognition also leads to a fictitious multiplication of hosts cited for a species of rust. Saccardo's "Sylloge Fungorum" contains many instances of this. I may, however, mention a specific instance taken from a later work, in which greater accuracy is expected, that of Sydow's "Monograph of the Uredineae." The second part of this work, just from the press, gives *Ferula dissoluta* and *Leptotaenia dissecta* as two hosts for a species of *Puccinia*, and yet both are names of the same plant. This is not a solitary instance. Such discrepancies ought not to occur, and largely would not if more importance were attached to the identity of the host.

There are many topics connected with this intricate and many-sided subject of the rusts that I should like to bring before you at this time, but to do so must prove wearisome, even to enthusiastic students of the family; and I fancy there are a few such in this audience. I will, therefore, content myself with a single additional topic, and even that must be treated briefly.

I wish to point out the profound influence that cytological studies are likely to exert upon the morphological, evolutionary and taxonomic conceptions of the rusts, when these are carried far enough to explain the significance of nuclear fusions in the different sorts of spores, and to indicate where in the life-cycle the sexual fusion occurs, or originally did occur. Much patient work has already been done by eminent investigators, Dangeard, Sappin-Trouffy, Raciborski, Poirault, Harper and others, and many facts have been brought to light, but we are more bewildered than edified by the results.

There seem to be a few things that we may accept as reasonably certain. One is that no close relationship exists between the Uredineae and the Ascomycetes, as advocated by DeBary, but that, on the other hand, the Uredineae and the Basidiomycetes have direct kinship. The nuclear fusions found in the teleutospore and in the basidium appear to be of similar nature, although probably without sexual significance.

The simple structure of the vegetative parts of the Uredineae should not mislead us into thinking that the family represents a reduced branch of the Basidiomycetes, for in all probability one family is as highly developed as the other, only one is along saprophytic lines of adaptation, and the other along parasitic. There are, in fact, some reasons for supposing that the Uredineae stand in the lead.

Of the various problems which cytological studies are expected to illuminate, none is more pressing than to discover the probable original function of the spermogonium. This body was at first held to be of the nature of the male sexual organ, hence the name, but all the studies and observations of recent times have done little to establish this view. Most students of the rusts ignore the structure entirely, or attach slight importance to it.

Without going into an argument, or even presenting opposing views, permit me to call attention to some significant facts regarding the spermogonium. These facts, it seems to me, tend to substantiate the assumption that we are dealing with the structure that originally functioned as the male reproductive body, but which long since in the developmental history, has ceased its functional activity, and become in all respects a disappearing organ. In the first place, in all cases where the life-cycle is known, the first body that is formed from the mycelium arising from teleutosporic conidia is the spermogonium. It begins the series of spore structures. In a full series the next structure is the aecidium, then comes the uredo and the amphispore if the latter occurs at all, both being asexual spores to meet requirements for rapid and certain distribution, and finally the teleutospore, having its characteristic mode of germination. The uredo and amphispores may be left out of this cycle, and often are, without disturbing the vigor and success of the organism. If the aecidium is omitted, however, the spore-form immediately associated with the spermogonia will be the uredo. These uredospores which arise along with spermogonia, however, differ in some physiological characteristics from those that arise later, having a greater disturbing influence upon the host, and are usually designated as primary uredo. It is significant in this connection that cytologically the aecidiospore and the uredospore are essentially alike. Going a step further, in what I consider reduction, and having both the aecidium and uredo omitted, we have the spermogonium appearing just in advance of the teleutospore. There is but one possible further reduction, and that is the suppression of the spermogonium, and we then have the whole cycle reduced to the simple formation of teleutospores.

To present the whole basis on which my argument rests, would take altogether too much time, and even to answer the queries and possible objections that will arise in the mind of every one who has some acquaintance with the subject, is equally out of question at the present, and I will instead give the conclusions at which I have arrived, and trust to some future opportunity for substantiating them.

I look upon the spermogonium as the beginning of the life-cycle, or more logically, the most important point in the cycle, in a fully developed rust organism. With it, and its associated spore-form, is always found the greatest exhibition of fungous vigor, showing some remnant of the original sexual power. The teleutospores I consider the close of the life-cycle, and the structure that is absolutely essential to the species. In the course of reduction, due to parasitism, the female sexual structures disappear first, then the male, and the final state is that of a purely sporophytic form.

If in this review of some of the problems confronting the uredinologist, I have more bewildered you than clarified the subject, you may be somewhat consoled by knowing that it is the frame of mind in which uredinologists themselves are usually plunged when they try to think out a connected and logical statement for these perplexing fungi. The subject at the present time is too much in shadow to present a concrete, recognizable picture.